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FURTHER STUDIES ON X CHROMOSOME BALANCE IN DROSOPHILA

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INTRODUCTION

IN AN earlier paper (PATTERSON, STONE and BEDICHEK 1935) the authors reported the effect of genic unbalance as it is revealed by aneuploid studies of the X chromosome. In that study hyperdiploid females were produced by adding duplications of varying lengths from one or the other end of the X chromosome. A report was made of the effect of these various duplications on the phenotype, the viability, and the fertility of the hyperdiploid females.

The results indicated that the phenotype and viability of these aneuploids depend, in general, on the section of the chromosome in duplicate. In addition, the fertility of the hyperploid females was found to be inversely proportional to the length of the duplicating piece. The only exceptions were observed in duplications which included the interval from *car* to the spindle fibre.

The results from the study of relatively long segments were not sufficient to show the exact effects of aneuploidy. Experiments were designed therefore to determine the effects of shorter segments. The use of short segments minimizes the difficulty arising from the summation effects which are unavoidable in the use of long duplications. In this as in the previous paper, the authors have not tried to differentiate the effects of aneuploidy that result from the various combinations of the fourth chromosome fragments, but have merely presented data which demonstrate the effect of the unbalance due to the aneuploidy of both X and IV chromosomes.

The genetic mechanism which controls the determination of sex in *D. melanogaster* has been studied by several investigators through an analysis of the effect of aneuploidy. PATTERSON (1931) has studied the effect of aneuploidy on the sex of the aberrant tissue in mosaics and gynandromorphs. DOBZHANSKY and SCHULTZ (1934) have studied the effect of additional X chromosome aneuploidy on triploid intersexes. This paper discusses the effect of aneuploidy on the determination of sex as it is revealed by X chromosome hypoploidy in the female and hyperploidy in the male.

MATERIAL AND METHODS

In order to obtain a series of short duplications, we have followed MULLER'S (1930) suggestion of combining two parts of different translocations in such a way that the left or right part of the one will form a

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short "overlap" with the right or left part respectively of the other. This method was used by DOBZHANSKY and SCHULTZ (1934). By the proper selections from among the several translocations, it is possible to duplicate in short intervals the entire X chromosome. The corresponding short deficiencies in the heterozygous female can be produced by selecting right and left parts which fail to meet.

Ten translocations were used as base stocks to produce the aneuploids studied. Of these, eight were employed in the previous work. These ten translocations involve either the X and IV, the X and II, or the X, II, and IV chromosomes. The origin of these stocks has been described by MULLER and STONE (1930), BOLEN (1931), and PATTERSON, STONE, BEDICHEK and SUCHE (1934). The stocks involving the X and IV are M5, broken at *w*; 9, broken between *rg* and *cv*; 17, between *t* and *lz*; W13, a deletion translocation, broken on the left between *lz* and *ras* and on the right between *bb* and the spindle fibre, to the right of all known genes, the middle portion (considered as constituting the right segment of the X) being inserted into the broken IV (MULLER, 1932); 8, between *fw* and *wy*; 4, between *sd* and *f*; 1, between *f* and *B*; and 13, between *fu* and *car*. In each of these cases except W13, the left portion of the X is attached to the right portion of the IV with its spindle fibre. Number 124 is a non-mutual translocation with the *v-g* sector deleted from the X and inserted into the II. In this case, the left break is between *ras* and *v* and the right between *g* and *pl*. Number 12 is a complicated double deletion. The section from a point between *sc* and *br* on the left and between *g* and *sd* on the right is deleted from the X and inserted into the IV. In addition, the *ct* locus is deleted from this portion of the X and inserted into the II (STONE 1934).

The gene map in crossover units (after Drosophila Information Service number 3) and the map of the X chromosome of the salivary gland, with indications of the genetic and cytological points of interchange of these various translocations, together with their unabbreviated nomenclature, are given in figure 3. Reference to this figure will make clear the position and extent of the duplication or deletion in the various combinations.

Two methods were used in combining parts of translocations to produce small duplications. In the first, gene markers situated close to the break were introduced into the translocations. Hyperploids were obtained as segregants from females heterozygous for the two translocations. The duplication was recovered in a male or female, depending on whether the gamete was fertilized by a Y- or by an X-bearing sperm. The success of this method depends on the fact that there is little or no crossing over in the region between the two points of breakage of heterozygous translocations, if this region is short, as BEADLE (1933) and STONE (1934) have

shown. Hyperploidy is sure if no males appear that would be the complementary crossover classes.

As an illustration of this method, 4L+8R hyperploid females may be obtained as segregants from the cross shown in figure 1. The hyperploid 4L+8R females are *v*, *non-wy*^{2}, *non-f*. They may be carried by selection

FIGURE 1

or balanced with an inversion. Crossing over between the loci of *v* and *wy*^{2} has not occurred in flies heterozygous for these translocations. Should crossing over have occurred, it could have been detected by the appearance of *non-v*, *wy*^{2}, *f* males. If such males had appeared, this method would not have been used.

In employing the second method, translocation males were crossed to *y v f* attached-X females. F_1 females hyperploid for one of the parts of the translocated X were mated to males containing a second translocation marked so that the short duplication-bearing males resulting from this cross could be detected. This method was limited to cases where the hyperploid female obtained from the first cross was fertile.

For example, the procedure of obtaining 1L+4R hyperploid males is shown in figure 2. In the F_2, the gray, round-eyed males possess 1L+4R. They are usually fertile when they receive a Y from the male parent.

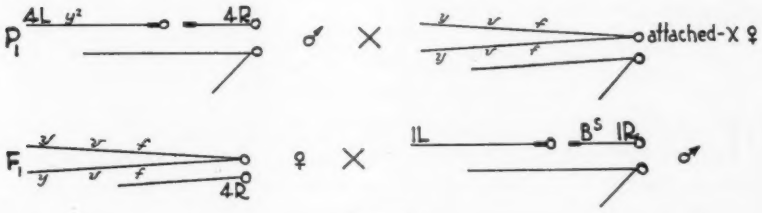

FIGURE 2

When a duplication-bearing male stock had been established, corresponding hyperploid females were obtained by crossing these males to normal females. In case the duplication caused sterility or was lethal in the male, it was isolated by the first method and carried in the heterozygous female. Breeding tests were made with the aneuploid females heterozygous for a normal chromosome, marked by the necessary recessive genes.

One hundred hyperploid males from each of the duplication stocks were tested for fertility. An equal number of hyperploid females and in addition an equal number of both male and female controls were tested. These controls were flies possessing the translocations from which the hyperploids were synthesized, heterozygous in the female and hemizygous in the male. In these tests, one hyperploid female was mated to three males in food vials. The males were marked in the several cases by the recessive genes necessary to distinguish between aneuploid and normal offspring. The control females were mated to normal males. Both hyperploid and control males were mated with *y v f* attached-X females, one male with three females. In each of these tests, the vials were examined on the third day after mating. The possibility of fertility was not regarded as sufficiently tested if the male or female test fly died on or before the third day. The vial containing the dead fly was not included in the group from which the percent of fertility was determined, unless the vial produced offspring. This procedure was consistent in all cases. The results give some index of the rate of mortality of the tested individuals. In the tables showing fertility tests, the "number mated" indicates the number of individuals that had to be crossed in order for 100 to be alive at the end of the third day.

To produce hypoploid females, females heterozygous for two unmarked translocations were crossed to males which carried in their X chromosome a recessive gene located in the interval between the two points of breakage and reattachment of the component translocations. The hypoploid segregants surviving showed this marker. The procedure for testing viability and fertility of the hypoploids was the same as that used to test hyperploid females.

EXPERIMENTAL RESULTS

(*a*) *Hyperploid females*

The results of the viability and fertility tests of the hyperploid females are recorded in table 1. The first column defines the duplication in terms of right plus left parts of its component translocation or translocations. For example, 9L+M5R indicates a duplication of the segment from the point of translocation of M5 to the point of translocation of 9 (see figure 3). The short duplications are listed in order from the left to the right of the X chromosome. In addition there are listed four longer duplications.

The second column gives the relative lengths of the duplicating segments measured on the drawing representing the map of the X chromosome from the salivary gland (MACKENSEN 1935). The third column gives the number of matings necessary to obtain one hundred cultures with the female still alive at the end of three days. The fourth column shows the

TABLE 1

Hyperploid females.

DUPLICATION	RELATIVE LENGTH	NUMBER OF MATINGS	PERCENT FERTILE	NON-HYPERPLOIDS		HYPERPLOIDS		PERCENT HYPERPLOID VIABILITY	
				♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
M5L	.131	103	74.0	1570	1573	921	123	58.7	7.2
9L+M5R	.114	103	48.0	1080	821	736	0	68.1	0.0
17L+9R	.150	108	96.3	1949	1954	2118	517	108.6	26.4
w13L+17R	.060	107	89.7	726	638	882	578	121.5	90.6
8L+w13R	.076	103	22.0	236	221	235	101	99.6	45.7
12L+8R	.093	(0 females occurred among 2000 inspected—2 were fertile)							
4L+12R	.062	105	93.0	1110	1331	1529	153	137.6	11.5
1L+4R	.084	101	100.0	1799	1683	1508	1102	83.8	65.5
13L+1R	.117	103	92.0	1146	1137	1247	657	108.8	57.8
13R	.109	102	97.0	1265	1307	2032	1822	160.6	139.4
w13L+9R	.210	101	50.0	243	228	194	0	79.8	0.0
4L+8R	.155	101	71.0	1061	1120	865	0	81.5	0.0
1L+w13R	.316	107	82.0	547	527	332	0	60.7	0.0
						M5L			
M5L+13R	.240	102	80.0	415	451	233	45	51.6	10.0
						13R			
						573	563	138.1	124.8
						M5L+13R			
						377	77	90.8	17.1

percentage of fertility derived from the one hundred cultures so selected. The term fertility is used to indicate ability to produce offspring, regardless of the number of offspring. The numbers of non-hyperploid and hyperploid progeny are listed in the four succeeding columns. Finally, the last two colums show the percentages of viability for the hyperploid flies, considering the viability of their non-hyperploid siblings as one hundred percent. These percentages are based on a comparison of the number of adult hyperploid flies with the number of their non-hyperploid brothers and sisters, respectively, which have developed in competition with them.

The percentage of fertility varies from 100 for duplication 1L+4R to 22 for 8L+w13R. If the percentages of fertility for the several intervals are compared, it is clear that their variations can not be correlated with the variations in length of the different duplications. For example the long duplication 1L+w13R is the aneuploid equivalent of the sum of the duplications 8L+w13R, 4L+8R, and 1L+4R. Nevertheless, it gives a fertility percentage of 82 which is higher than that for either of the intervals 8L+w13R and 4L+8R, but considerably lower than the 100 percent fertility for interval 1L+4R. Again, duplication M5L+13R is a combination of duplication M5L and duplication 13R, which separately give fertility percentages of 74 and 97, respectively. The M5L+13R fertility

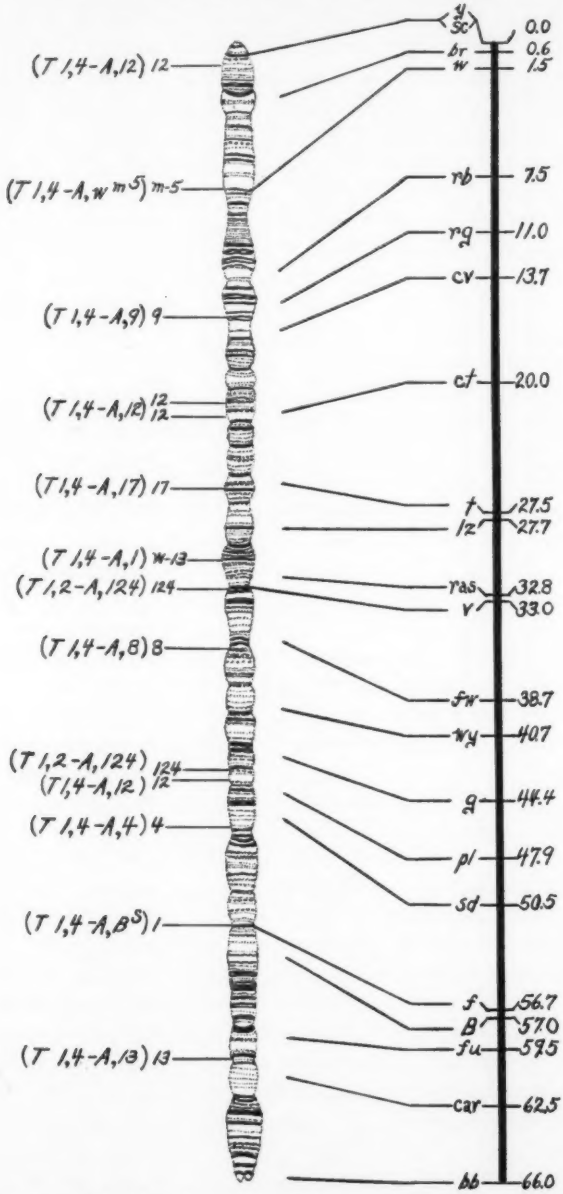

FIGURE 3. The points of interchange of the various translocations are indicated on the map of the X chromosome drawn from the salivary glands (MACKENSEN 1935). The genetic map is taken from Drosophila Information Service number 3. Where the exact cytological locus of a gene is known, this locus on the cytological map is connected with the genetic locus. The approximate cytological loci of the other genes are indicated.

percentage of 80 is intermediate between those for the two shorter intervals.

Because of the nature of the combinations used, controls were of limited value. However, control breeding tests were made with females heterozygous for each of the translocations. This was done in order to determine whether there was any dominant effect on fertility due to the translocation itself. The results of the tests, which are given in table 2, do not show any such influence.

TABLE 2

Females heterozygous for the translocation.

STOCK	MATED	PERCENT FERTILE	FEMALES	MALES
M5	100	100.0	4626	3672
9	100	100.0	4843	3329
17	95	100.0	1309*	1098*
W13	105	97.0	4213	2948
8	112	97.0	3490	2796
4	102	99.0	3309	3187
1	102	99.0	3081	2933
13	100	99.0	3748	3286

* Sample count from 60 vials.

With the exception of 12L+8R, the viability of the hyperploid females varies from 58.7 percent for M5L to as high as 160.6 percent for 13R in one test and 138.1 percent in another. Duplication 12L+8R has a viability of less than 1 percent; indeed, only nine were found among approximately 2000 females examined. Probably this low viability is due to the deficiency in 12L of the extreme left end of the X chromosome. This region includes the factor which PATTERSON (1932) has shown to be necessary for the survival of diploid females. Especial attention should be directed to three of the duplicating intervals. Duplication 8L+W13R, which includes the *v-m* section, shows practically a normal viability percentage (99.6). Females carrying 13L+1R, with a viability percentage of 108.8, are more viable than their non-hyperploid sisters. The females carrying the terminal duplication 13R (*car* spindle fibre end) are extremely viable, with percentages 160.6 and 138.1 in two different tests. This increased viability is shown in the results obtained from duplication M5+13R. In breeding these hyperploid females, the F_1 females hyperploid for only M5L are 51.6 percent as viable as their normal sibs, whereas those with only 13R have a comparative viability of 138.1 per cent. The aneuploids having both fragments show an intermediate percentage of 90.8.

(*b*) *Hyperploid males*

Males survived with a duplication of any one of nine of the ten small intervals into which the X chromosome was divided. No males survived hyperploid for the interval between 8 and 12. Neither 4L+8R nor 124M survived as X+duplication, whatever the sex of such an individual would be. Other tests with 124 were reported in the former paper (PATTERSON et al, 1935). Egg counts and hatching experiments, although not tabulated, show that flies with one X chromosome plus the duplication resulting either from 4L+8R or 124M (midregion on II) die before larvae emerge from the eggs. For example, 58 eggs from a female hyperploid for 124M gave 16 dead eggs; 13 normal females, 13 normal males, 9 hyperploid females, and 7 larvae which were probably hyperploid females that did not survive the pupal stage. Further, some twenty larvae which proved to be aneuploids all had 2X+124M, as determined from their salivary gland chromosomes.

The percentages of viability for the hyperploid males are given in the last column of table 1. In the experiments listed here, 9L+M5R males were not obtained. Other experiments, however, show the viability of males carrying this duplication to be less than one percent. The highest viability was found in males hyperploid for region 13R, representing the right end of the X chromosome. Their viability percentages were 139.4 in one test and 124.8 in another. On breeding M5+13R hyperploid females, hyperploid males occurred in these ratios (in percent): M5, 10.0; 13R, 124.8; M5+13R, 17.1.

The results of the breeding tests of the males carrying the nine surviving duplications are given in table 3. The fertility percentages vary

TABLE 3

Hyperploid males.

DUPLICATION	RELATIVE LENGTH	NUMBER OF MATINGS	PERCENT FERTILE	NON-HYPERPLOIDS		HYPERPLOIDS	
				♂♂	♀♀	♂♂	♀♀
M5L	.131	107	78.0	1126	1606	185	1007
9L+M5R	.114	144 (79 dead)	41.6	—	(187)*	4	(187)*
17L+9R	.150	132 (41 dead)	1.1	—	3	1	2
w13L+17R	.060	104	89.0	—	1873	1876	1303
8L+w13R	.076	103	89.0	—	631	479	525
4L+12R	.062	123	2.0	—	10	3	12
1L+4R	.084	101	91.0	—	766	670	1208
13L+1R	.117	103	42.0	—	17	26	73
13R	.109	105	20.0	69	(158)*	24	(158)*

* Hyperploid and non-hyperploid ♀ ♀ could not be distinguished.

TABLE 4

Translocation males.

STOCK	MATED	PERCENT FERTILE	NON-HYPERPLOIDS		HYPERPLOID ♀♀	
			♀♀	♂♂	LEFT	RIGHT
M5	113	98.0	2146	1188	1084	58
9	119	75.0	1846	912	1064	15
17	75 (no dead)	93.3	130	133	43	21*
W13	104	88.0	1950	2228	1176	632
8	106	94.0	1833	1801	706	873
4	100	94.0	2206	2198	118	2627
1	101	97.0	1555	1612	30	2301
13	100	91.0	(1853)†	718	18	(1853)†

* Sample count from 10 matings.

† Hyperploid and non-hyperploid females could not be distinguished; total = 1853.

from 1.1(17L+9R) to 91.0 (1L+4R). The relatively high percentages of 89.0 for intervals W13L+17R and 91.0 for 1L+4R are somewhat lower than the average for non-hyperploid males. The most striking reductions in fertility are found in regions 17L+9R (1.1 percent) in the left, and 4L+12R (2.0 percent) and 13R (20.0 percent) in the right end of the X chromosome. In table 4 are shown the male control fertility percentages of eight of the translocations. With two exceptions, the percentages obtained are practically as high as those usually found for normal males. Stock W13 gives the slightly reduced percentage of 88.0, but 9 shows the greatest reduction in fertility (75.0). That this low percentage was not due to some environmental influence was shown by another test which gave for 9 a fertility percentage of 71. There must be something in the nature of this translocation that results in lowering the fertility of males which carry it. Females heterozygous for 9 are 100 percent fertile (table 2). Hence, the effect cannot be dominant unless it is a male semi-sterility factor. Probably the reduction in fertility in those hyperploids which involve 9 is not due to the effect of the translocation itself.

The effect of the aneuploidy of short sections upon phenotype was not so accurately measurable as viability and fertility. The effect was slight in most cases. Nevertheless, in several stocks, the external genitalia of some of the hyperploid males were rotated. The rotation, which varied from about 20° to 360°, was thought to have contributed to the sterility of such hyperploid males. Table 5 shows the numbers of the various aneuploid males with rotated and non-rotated genitalia. Males carrying 17L +9R, which are only 1.1 percent fertile, show the most marked degree of rotation. In this case, 73.3 percent of these males have rotated genitalia.

TABLE 5

Rotation of genitalia.

DUPLICATION	NUMBER NORMAL	NUMBER ROTATED	PERCENT ROTATED
M5L	80	9	11.2
9L+M5R	27	0	0.0
17L+9R	16	44	73.3
w13L+17R	100	10	10.0
4L+12R	17	1	5.8
1L+4R	100	0	0.0
13L+1R	100	0	0.0
13R	90	1	1.1

However, the next highest percentages of rotation, 11.2 and 10.0, are found in stocks M5L and w13L+17R, respectively, with the comparatively high percentages of fertility of 89.0 and 78.0. The structure of the internal genitalia of rotated M5L and w13L+17R males was found to be normal except that the penis apparatus was rotated to correspond to the external displacement. However, 7 out of 44 males of the 17L+9R stock which were dissected had abnormal testes. The abnormalities were reduction in size, shortening and thickening with reduction in coiling, or reduction in thickness without reduction in coiling. The anal plates were normal in all stocks.

(*c*) *Hypoploid females*

Only four hypoploid stocks survived. The results of experiments involving these are shown in table 6. In all cases, fertility and viability are

TABLE 6

Hypoploid females.

COMPOSITION OF HYPOPLOID ♀	RELATIVE LENGTH	NUMBER OF MATINGS	FERTILE	PERCENT FERTILE	NON-HYPOPLOIDS		HYPOPLOIDS
					♀♀	♂♂	♀♀
$\frac{M5L+9R}{rb}$	.114	67 19 dead	9	18.7	11	10	4
$\frac{17L+w13R^*}{l}$	.060	26 11 dead	2	13.3	5	2	
$\frac{w13L+8R}{v}$	.076	113 15 dead	0	0.0			
$\frac{13L}{car}$	.109	59 23 dead	8	22.2	13	25	2

* These hypoploid females were detected by their phenotypic resemblance to known hypoploids, where *lz* was used to demonstrate hypoploidy.

very low. Copulation in hypoploid females is abnormal, for often the male and female fail to separate, leading to the death of the flies. Only 17L+w13R failed to show marked phenotypic abnormalities. Females hypoploid for the interval between w13 and 8R are smaller than normal, and their wings are outstretched. Deficiency of the region between M5L and 9R causes, in addition to these defects, smaller and thinner bristles, notched wings, and rough eyes. The mutant *rb* introduced by the male parent was exaggerated. Females lacking the 13R region in one of their X chromosomes possess minute bristles, small body size, and large rough eyes with an exaggeration of *car* eye color. All of the hypoploid females hatch late. In several of the breeding tests, females produced larvae which failed to reach maturity. In this case, these were considered fertile.

DISCUSSION

Viability and fertility are variable and their true indices are only approximated in these experiments. This is especially true of fertility since only 100 individuals were tested in each case. Several factors influence this variability. For example, the viability index of 13R hyperploid females is different in two experiments using different stocks (138.1 and 160.6). Certain of the experimental facts may be reviewed to illustrate the situation.

Hyperploid females are somewhat more viable and more fertile (with one exception, stock 8L+w13R) than the corresponding hyperploid males. However, all hyperploids were fertile to some degree. Hypoploid females are extremely inviable and infertile. Nevertheless, the extent of the effect of the aneuploidy had to be determined experimentally in each case.

The fertility of hyperploid females is a function of the quality rather than of the quantity of the duplicating chromosome segment. For example, 92 percent of the females hyperploid for 13L+1R are fertile. This duplication is 0.117 part of the chromosome as measured on the cytological map of the X chromosome. Only 48 percent of the 9L+M5R hyperploid females are fertile, although the relative length is about the same, 0.114. A similar lack of relation between length of duplication and fertility holds true in the tests with hyperploid males. Thus the duplication w13L +17R is proportionately 0.060 the length of the X chromosome, and of the males possessing this duplication 89.0 percent are fertile. Of the males which have the 4L+12R duplication, with a relative length of 0.062, only 2 percent are fertile.

Likewise, percentage of viability depends upon the particular region rather than upon length of duplication in both male and female hyperploids. This may be illustrated by females carrying the duplication 9L +M5R, of relative length 0.114, of which 68.1 percent are viable. Females

hyperploid for 13R, length 0.109, have a viability percentage of 160.6.

There is no consistent relation between the degree of fertility of the hyperploid males and the degree of fertility in females hyperploid for the same region of the X. Sometimes, the two are approximately the same, as in M5L, where 74.0 percent of the females are fertile as compared with 78.0 percent of the males. In one stock, 8L+w13R, the hyperploid female has a considerably lower fertility than the corresponding hyperploid male, where 22.0 percent of the females are fertile and 89.0 percent of the males. Finally, there are cases in which the reverse is true, the fertility of the male being much lower than that of the female. One example of this last relation are the flies hyperploid for 13R. Here 97.0 percent of the females are fertile as compared to 20.0 percent of the males.

In the case of viability there is no consistent relation between the degree of viability of males and females hyperploid for the same segment of the X. This is clearly shown in M5L, in which the hyperploid females have a viability 58.7 percent as high as normal as compared with 7.2 percent for the hyperploid males. This is also the case of 8L+13R, where the hyperploid females are 99.6 percent viable, and the hyperploid males only 45.7 percent.

The fact that viability and fertility are not predictably related is self-evident. In the case of M5 hyperploid males, 7.2 percent are viable but 78.0 percent are fertile. In contrast to this 13R hyperploid males are 139.4 percent viable but only 20.0 percent are fertile. Again, we find among the hyperploid female stocks that 8L+w13R has a viability percentage of 99.6 as compared with a fertility percentage of 22.0.

Several experiments show the relation between longer duplications and their component parts. There are several examples in relation to fertility:

(1) In the w13L+9R overlap hyperploids, 50.0 percent of the females are fertile as compared to the component equivalent of 17L+9R (96.5 percent fertile), plus w13L+17R (89.7 percent).

(2) 1L+w13R with a fertility index of 82.0 percent may be compared to its component intervals 8L+w13R (22.0 percent), + 4L+8R (71.0 percent), + 1L+4R (100.0 percent).

(3) Eighty percent of the females having two X chromosomes and in addition the M5L and 13R fragments are fertile. Seventy-four percent of M5L hyperploid females are fertile, and 97.0 percent of those hyperploid for 13R.

These examples of fertility illustrate that the fertility of a long duplication cannot be predicted from a knowledge of the fertility of hyperploids the sum of whose duplications is the aneuploid equivalent of the long duplication. This is true also of viability.

There are wide variations from expectation on the assumption of simple

cumulative effects, especially in view of the fact that increasing the extent of hyperploidy may increase the fertility of the tested females as, for example in (2) above. These variations serve to indicate the complexity of this balanced system. Fertility and viability are not merely functions of the interchromosomal balance between genes of the X and those of the autosomes. The effects of aneuploidy demonstrate the intricacy of the additional intrachromosomal gene balance of the X chromosome.

The effect of certain of these aneuploids on viability and fertility may be related to the possible evolutionary significance of small duplications. In several cases the viability of hyperploid females exceeds normal: for example, 4L+12R with 137.6 percent, and 13R with 160.6 percent (or 138.1 percent). The males possessing these duplications were of lower fertility and viability except 13R, with a viability of 139.4 percent. The minute duplications discovered by BRIDGES (1935) and OFFERMANN (1936) by means of the salivary gland technique may well have had such an initial advantage as the hyperploid females in these cases.

SEX DETERMINATION

Several methods have been used to study the mechanism of sex determination. One of these methods is race crossing, another is the interpretation of the effects of aneuploidy, and still another is the use of gene mutations. The results of such studies on various forms have given rise to two theories of sex determination. One of these implies that sex is determined by the interaction of a few main genes (with or without modifiers), while the other theory assumes that sex is determined by multiple factors. Both types of gene systems are known to be operative, and it therefore becomes necessary to determine experimentally which system exists in any particular form.

There are two ways of determining whether an individual is a male, a female, or an intersex. One way is the test of fertility, and the other is a study of the phenotype of the individual with regard to the secondary sexual characteristics. Both tests are desirable, but they must be used separately in certain cases. In order to interpret the data available on sex determination in *D. melanogaster*, one must consider the work that has been done on other insect forms, especially the investigations reviewed below.

GOLDSCHMIDT has shown that in pure races of *Lymantria dispar*, sexual differentiation is controlled by a principal male-tendency gene, *M*, in the X chromosome, and a female-tendency influence, *F*, in the cytoplasm. As the female is heterogametic, the complex *F MM* is a male and *F M* is a female (GOLDSCHMIDT 1934). In addition, a few autosomal modifiers of the primary male gene have been found. This method of sex determination was demonstrated by interracial crosses which show that the male sex

genes in the X chromosome form a series of multiple alleles which differ in potency and are additive in effect. The female tendency factors are in balance with their respective male tendency genes in any pure race. Certain interracial crosses produced diploid intersexes. These ranged from sex reversal males to sex reversal females.

From the results obtained from breeding hybrids of *Lymantria dispar*, GOLDSCHMIDT concluded that sex was determined by the factors *F* and *M*. If any modifying factors existed, they were identical in the several races. This represents a single complementary male and female system, apparently without modifiers. GOLDSCHMIDT used secondary sexual characteristics and fertility tests when possible to determine the potencies of the sex factors in the several races.

Several comparable systems of multiple alleles have been described. In *D. melanogaster*, MOHR (1932) has studied the vestigial allelic series, and MULLER (1932, 1935) has discussed experiments with the white series. In the latter case MULLER has shown that there are two normal alleles of different potencies in the American and Russian races of *D. melanogaster*. HARLAND (1936) has reported work with the crinkled dwarf mutants in several species of cotton. He finds that the main gene is represented by a series of alleles of different potencies in the several species. However, the species differ in that each has its own specific and different set of modifiers of the main gene. Cotton differs, then, from *Lymantria dispar* in that each main gene has an easily demonstrable and important set of modifiers.

WHITING (1935) has proposed a theory to interpret the mechanism of sex determination in Hymenoptera. This theory is based on the results of experimentation with *Habrobracon juglandis*. WHITING assumes that there are two homologous sex chromosomes, an X and a Y. These chromosomes differ only in respect to allelic sex factors. The X has *Fg* and Y has *fG*. The factors *f* and *G* are completely linked, or represent only one gene. A female is formed by the combination *Fg* (X) and *fG* (Y). Either *Fg* (X) or *fG* (Y) is a male. In crosses between unrelated strains, selective fertilization always occurs by the orientation of the maturation division spindles and chromosomes in the female in such a way that if the sperm contains an X, the female pronucleus will always contain a Y, or vice-versa. That is to say, the differences between two pairs of alleles can determine the orientation of the chromosomes or the spindle in the reduction division. However, in closely related strains, this kind of selective fertilization sometimes fails to function properly so that XX or YY combinations may be formed. These combinations produce the exceptional diploid males found in Habrobracon. This hypothesis was supported by the discovery of a sex-linked gene, fused. In most of the tests which WHITING reported, this gene segregated in a manner predictable on the assumption that fused was

linked with *fG* or *Fg*. WHITING's theory is essentially a special single factor interpretation of the mechanism of sex determination.

SNELL (1935) proposed a modification of WHITING's theory of sex determination. He postulated that there are several genes concerned in sex determination, which are not necessarily linked. To support this modified theory, SNELL called attention to the fact that BOSTIAN (1934) had shown that the rate of occurrence of biparental males could be modified by selection. He considered that in different strains the groups of genes determining sex might differ. On this basis SNELL predicted that fused would not always appear to be sex-linked when outcrossed to unrelated males. DORDICK (1936) has verified this prediction experimentally. SNELL assumed that the female is heterozygous for a number of genes. The heterozygous condition produces a female because the female-determining genes are dominant and cumulative in effect. Selective fertilization is therefore unnecessary. Haploids are males because in one set of chromosomes there are not enough of the cumulative female genes to dominate the reaction. Biparental diploid males occur on inbreeding due to recombination. In those combinations that have a relatively large number of the recessive alleles of the female-determining genes, the male-tendency genes dominate the reaction. Theoretically, haploid females could be produced by selection in the other direction. Such females, or diploid females for that matter, which possessed or acquired the ability to omit the reduction division as has the male, could give rise to pure female lines. These, by mutation in haploids, or by crossing over and segregation in the diploids, as well as by an occasional reduction division, could give rise to males. Some species of Hymenoptera which are all or nearly all females may have arisen in this way. SNELL's theory assumes that sex is determined in Habrobracon by multiple factors.

Either WHITING's or SNELL's theory may be the explanation of sexual differentiation in Habrobracon. Both may be regarded as specific examples of a more general principle, which implies that sexual differentiation is dependent upon the difference in cumulative effectiveness of the male- and the female-tendency genes. Normally, in Hymenoptera the female-tendency genes are cumulative, whereas those for maleness are not. A mutation, or mutations, causing an increase in effectiveness of two doses of the male genes or a decrease in effectiveness of two doses of the female genes, could condition the formation of diploid males. Mutations in the opposite direction might cause haploid females to appear. Therefore, regardless of the more recent data presented, it is still unnecessary to rely upon heterozygosity for sex determination in Hymenoptera, nor can a final decision be made between single and multiple factors as the mechanism.

LEBEDEFF (1934) has reported several mutations which affect sex determination in *D. virilis*. The main gene, a recessive mutation *ix*, is located in the third chromosome. When *ix* is homozygous, diploid individuals with two X chromosomes are phenotypic males. There are several modifiers of this gene which cause the action of the gene to be less pronounced, resulting in six intergrades. Some of these intergrades resemble gynandromorphs, intersexes, and hermaphrodites. The sex reversal males are sterile, but this may be due to the absence of a Y chromosome. There is the possibility that the *ix* mutation is a neomorph, in the terminology of MULLER (1932), and acts in an entirely new direction from its normal allele. This is an improbable assumption in view of the low frequency of the neomorphic type of mutation. The action of *ix* may be used to interpret the function of its normal allele.

The situation is this, in regard to the *ix* gene in *D. virilis*:

(1) 1X:2A = male, when the genotype is +/+, *ix*/+, or *ix*/*ix* in the third chromosome.

(2) 2X:2A = female, when the genotype is +/+ or *ix*/+ in the third.

(3) 2X:2A = sex reversal male, when the genotype is *ix*/*ix* in the third, without modifiers.

(4) 2X:2A = sex reversal incomplete, when the genotype is *ix*/*ix* in the third, with modifiers.

When genotype (2) is a female and (3) is a male, sex is determined by the gene *ix* and its normal allele. On the basis of these facts sex in *D. virilis* may be determined by the normal allele of *ix*, using the relation 1X:2A and 2X:2A as part of its mechanism. The normal allele of *ix* would be considered the primary sex factor. Even though *ix* were only a neomorph, it is a gene capable of determining maleness in opposition with the 2X:2A condition which normally results in a female. These experiments are the nearest approach to the action of a single gene in sex determination in Drosophila.

Several studies have been made in *D. melanogaster* in an attempt to decide between a single or multiple factor system of sex determination.

PATTERSON (1931) reported a number of gynandromorphs and mosaics in which the aberrant areas were due to a loss of part of one X chromosome. The aberrant areas of these proved to be male when the *m-g* section was lost, and female when it was present. Since the *m-g* sector is in the middle of the chromosome, and since a relatively large part of the chromosome was missing in each case, no final conclusion could be drawn as to the specific action of the genes in this region of the chromosome.

BRIDGES' (1932) study of triploid intersexes led him to support the multiple factor system. Bridges assumed that sex is determined by the interaction of a number of female-tendency genes most of which are in the X

chromosome and male-tendency genes most of which are in the autosomes. A change in the amount of either X chromosome or autosome shifts the balance. DOBZHANSKY and SCHULTZ (1934) tested this hypothesis by comparing 3A:2X intersexes with their sibs 3A:2X plus different fragments of the X chromosome. Long duplications produced extreme female-type intersexes, resulting in fertile hypotriploid females in some cases.

The ease with which the type of intersex may be changed by temperature or by modifying genes leads GOLDSCHMIDT (1935) to doubt the decisiveness of the intersex test for sex genes. DOBZHANSKY and SCHULTZ take the opposite view. If the type of intersex is influenced readily, this shift in intersex type should be particularly adapted to locate sex genes. GOLDSCHMIDT considers the effect of hyperploidy in the 1X:2A individual or hypoploidy in the 2X:2A individual the more critical tests. He points out that hyperploid females indicate nothing in regard to the question of single or multiple sex genes in Drosophila. The present work, substantiating that view, shows that diploid females hyperploid for short sections of the X are practically normal. The various hyperploid females studied demonstrate that aneuploidy causes the expression of characters such as rough eyes and clipped wings in triple-X females. Sterility, probably, is caused by the same phenomenon. These results do not substantiate PATTERSON, STONE, and BEDICHEK (1935) in their former assumption that the genes affecting fertility are probably the multiple factor female-determining genes proposed by BRIDGES.

The phenotypic abnormalites of these aneuploids cannot be interpreted as positive shifts in the sex of the organism. Males hyperploid for different short duplications show no intersexual or female characteristics. Aneuploidy in general, and not intersexuality, is assumed to be the explanation for the rotation of genitalia and other abnormalities, especially in view of the fact that each type of hyperploid male is fertile. Hypoploid females showed no tendency toward maleness. However, DOBZHANSKY and SCHULTZ (1934) and DOBZHANSKY (1935) argue that the threshold for a change in direction of sexual differentiation is higher in diploids than in triploid intersexes. Consequently, if a number of genes control sex, a small duplication of the X in the male or a small deficiency of the X in the female need not be expected to produce a reversal in sex. Certainly none of the diploid aneuploids reported here is distinctly intersexual. However, essentially diploid intersexes (as judged by the phenotype, which is the method of determining intersexuality) are produced by the action of *ix* and its modifiers in the related form, *D. virilis*. There is no reason to believe that diploid intersexes would be inviable in *D. melanogaster* due to intersexuality.

A primary factor and multiple factors are the two extreme systems possi-

ble for sex determination. There are numerous steps between them where one or more modifying factors influence the effect of the main gene. The *crinkled-dwarf* system in cotton illustrates a main gene with an extreme modifying system. A priori, any one of these systems might determine sex. Several of the possible systems will now be considered in the light of the experimental data that has been accumulated.

In any of the systems both the female factor or factors and the male factor or factors are cumulative in effect because 1X:2A is a male; 2X:2A, a female; 2X:3A, an intersex, and 3X:3A, a female.

(1) If there is a primary sex factor so that 1 factor (in the X): 2A is a male and 2 factors: 2A is a female, it must be in the *g* region of the chromosome between 12 and 8 in figure 3. Hyperploid males rule out all other sectors. This would be a single factor comparable to the male factor in *Lymantria dispar*. An even more extreme system can exist in Drosophila. 2X:2A with *ix* heterozygous is a female and 2X:2A with *ix* homozygous is a male in *D. virilis*. This is a system of sex determination dependent on allelic genes, without even the ordinary X chromosome mechanism.

(2) The activity of a modifying system may be necessary in complementing the activity of one or two doses of the primary gene. Several of the possibilities in the diploid are: (a) If the majority of the remaining X chromosome genes concerned with sex are diploid, two doses of the sex gene will produce a female. One dose of the main gene will produce a male even if the modifying system is diploid. Hypoploid females representing each region would negate this hypothesis. Only four of the ten intervals studied lived as hypoploid females. (b) One sex gene and a haploid complement of modifiers produces a male. One sex gene with a diploid set of modifiers produces a female; and in addition two sex genes with even a haploid set of modifiers produces a female. This supposition is ruled out for nine of the ten intervals of the X, since hyperploid males survive. (c) One or two doses of the primary sex gene plus the diploid complement of X-chromosome modifiers produces a female. Either one or two doses of the primary genes plus haploid modifiers produces a male. Neither hyperploid males nor hypoploid females will rule out this possibility.

The possibility remains that the primary female factor lies in the autosomes, a situation similar to the system with the normal allele of *ix* in *D. virilis*. In the examples above, 2c is similar to the situation with the normal allele of *ix*, except that the main gene is postulated to be in the X. 2b is a modification of this.

The final alternative is that of a multiple factor system. The data on aneuploids in this paper do not give much evidence for or against this hypothesis. Certain factors in the X are more necessary in the diploid condition for viable and functional females than effective in shifting males

toward intersexuality. This can be inferred from contrasting hyperploid males and hypoploid females. The work of DOBZHANSKY and SCHULTZ (1934) has shown that there are several modifiers of the main sex factor or several multiple factors in various parts of the X chromosome. Neither their work nor this permits a decision regarding the relative importance of these genes in the diploid.

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SUMMARY

1. The effect of aneuploidy of relatively short segments of the X chromosome in diploid individuals in *D. melanogaster* on viability, fertility, and sex is reported.

2. With certain exceptions, hyperploid females are more viable and fertile than hyperploid males, which in turn are more viable and fertile than hypoploid females.

3. Viable and fertile hyperploid females and males were obtained for each region of the X chromosome except the *g* region.

4. The type of gene system which determines sex in *D. melanogaster* is unknown.

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GENETIC AND ENVIRONMENTAL FACTORS AFFECTING THE DEVELOPMENT OF THE SEX-COMBS OF DROSOPHILA MELANOGASTER

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INTRODUCTION

TEMPERATURE has long been recognized as a fruitful tool for the analysis of developmental processes. The Mendelian interpretation of heredity has caused many experimental embryologists to focus their interest upon the development of characters whose genetic nature is more or less known. During the past few years much has been gained from temperature studies made upon the development of the eyes of Drosophila in which the Bar series has furnished a variety of allelomorphic differences. To the knowledge of the author, no thoroughgoing temperature studies have been made upon a sex-limited character. The sex-comb of Drosophila seems to present possibilities for such an analysis. The present investigation has been made as a preliminary survey of several stocks of inbred Drosophila. Although no genetic factors primarily influencing the sex-comb were used, the effect of the infrabar gene has been found to furnish interesting results.

MATERIALS AND METHODS

The stocks used in these experiments were all inbred for at least 10 generations previous to the present investigation. The Bar stock had been inbred for over 200 generations. The flies were cultured on the usual banana-agar-yeast medium in 8-dram homoeopathic vials. Temperature was controlled by means of automatic electric incubators housed in the warm and cold temperature rooms of the Zoological Laboratory of the University of Illinois. Recording apparatus showed that the temperatures did not fluctuate more than ± 0.3°C during any of the experiments. The same parents were used to produce offspring of each stock for both the 17°C and 27°C experiments.

After emergence the flies were preserved in 80 percent alcohol and were later dehydrated in absolute alcohol. The legs were then dissected off and mounted in euparal. The tarsi and the sex-combs were studied under the compound microscope.

Recounts of the teeth in the sex-comb showed less than 1 percent of error, and remeasurement of the tarsi showed an equally small error. Bananas of a constant degree of ripeness were used in an attempt to reduce

differences in food to a minimum. For each stock the food for the 17°C and the 27°C experiments was obtained from a single mixture. All vials which showed more than 20 or less than 5 pupae were discarded except in the experiments for determining the effects of population size.

EXPERIMENTAL DATA

The effect of population size

At the time of pupation of the Bar stock the vials were separated into groups according to the number of pupae present. In the 27°C experiment they were classified into two groups of 1–20 and 20–45 pupae. The group with 1–20 pupae was subdivided into those having 1–5, 5–10, 10–15 and 15–20 pupae. The mean number of teeth in the sex-comb and the tarsus length of these four groups were not found to be statistically different. Similar groups of the 17°C experiment of the Bar stock gave the same result. In the 27°C experiment, in vials having more than 20 pupae, the first 20 flies to pupate showed a reduction in the size of the tarsus and the number of teeth in the sex-comb as compared with those raised in populations which did not exceed 20 per vial. Those emerging after the first 20 were found to be further reduced in both of these characters. Consequently all vials having more than 20 pupae were discarded from the experiments in which the effects of temperature were determined.

Unusual sex-combs

Among the several hundred sex-combs observed, two interesting types appeared which deviated from the normal (fig. 1). In the Bar stock about 2 percent of the individuals in the 17°C and 1.5 percent in the 27°C experiments showed a discontinuity in the serial arrangement of the teeth. It appeared that a tooth had failed to develop leaving a small gap. However, closer examination of the data indicates that this conclusion is probably erroneous since the average number of teeth in these variants of the 27°C experiments is almost one tooth greater than the average for the normal, while the average of the variants of the 17°C experiments is almost one tooth less than the normal. The position at which the split in the sex-comb occurs is irregular and is possibly due to the intercalation of non-tooth producing tissue during development. In no case was the variant found to be bilateral.

Another type of variant was found in the Bar-infrabar stock. About 1 percent of the individuals of the 17°C experiment carried a jumbled arrangement of the teeth. Sex-combs such as these were not found in the same stock reared at 27°C. This variation was in no case found to be bilateral.

One gynandromorph was observed in the Bar stock. It had 10 teeth in the sex-comb of the right leg and no sex-comb was found on the left leg.

Correlation of the right and left side of the same individuals

The data were derived from the wild stock reared at 27°C. The number of teeth in the sex-combs and the tarsus length were studied in 285 pairs of legs.

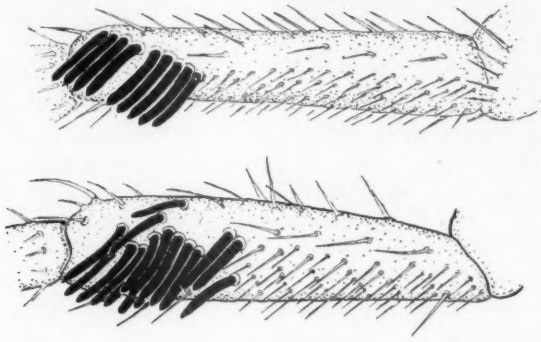

FIGURE 1. Two unusual types of sex-combs. Camera lucida drawings.

Sex-combs. Early in the investigation it was noted that the number of teeth in the sex-combs often differed on the two sides of the same individual. The mean number of teeth in the sex-comb of the right side was found to be $10.57 \pm .03$ and on the left side $10.49 \pm .03$. The mean of all the sex-combs (both sides) of individuals which were alike on the two sides was $10.57 \pm .03$ and the mean of all the sex-combs (both sides) of individuals having unlike sex-combs was $10.39 \pm .03$. The coefficient of correlation of the number of teeth in the sex-combs on the two sides was found to be $+0.20 \pm .04$. About 36 percent of the individuals had the same number of teeth on both sides; 47 percent had a difference of one tooth; 15 percent a difference of two teeth; and 2 percent a difference of three teeth.

Tarsus length. The coefficient of correlation of the tarsi of the right and left sides was found to be $+0.55 \pm .03$. About 62 percent of the individuals had the same length of tarsus on both sides; 38 percent differed by one unit (.0055) on the two sides; and 1 percent differed by two units. The length of the right tarsus was $10.08 \pm .02$ units, the left $9.99 \pm .02$ units. The mean of all those having tarsi equal on the two sides was not found to be statistically different from those having unequal lengths of tarsi on the two sides. The difference of the two means was 1.59 times the probable error of the difference.

Correlation of the length of the tarsus and the number of teeth in the sex-comb of the right side

The correlation coefficients for the number of teeth in the sex-comb and the length of the tarsus are given in table I. All the coefficients are positive but with the exception of Bar-infrabar they do not fall within the limits which would be considered statistically significant by the usual criterion. However, IMAI (1933) has called attention to the fact that coefficients of highly inbred stock of Drosophila should be interpreted on a different basis than that usually used in cases of heterozygous stocks. It is therefore possible that the data may be interpreted as showing a low positive correlation. It must be pointed out that positive correlation in this case does not indicate that the two structures are genetically related in the strictest sense, for the tarsus is apparently not to a significant degree affected by the Bar and infrabar genes, as is shown in the temperature studies. In an overcrowded population of the wild stock reared at 27°C the coefficient of correlation was found to be $+.165 \pm .02$ and this seems to indicate that population size does not significantly alter the coefficient of correlation for these characters.

The effect of temperature upon the mean

Tarsal length. Table I gives a tabulation of mean tarsal length for the four stocks in which this structure was studied. Since these stocks had not been subjected to selection it is highly probable that they all carried modifying factors as well as the known genetic differences; this may account for the differences in length in the four stocks. It is obvious that there is a similarity in the reaction of this character to the effects of the two temperatures at which it was studied.

The number of teeth in the sex-comb. Referring again to table I it is seen that the stocks which have the infrabar gene react to temperature in the opposite manner to those not having the infrabar gene. It should be called to mind that the eye facet count in infrabar varies directly with increase in the temperature at which the animals are allowed to develop (LUCE 1931) while the present data show that the number of teeth in the sex-comb of this stock varies inversely with temperature. On the other hand, the facet count of Bar (KRAFKA 1920, DRIVER 1926) varies inversely with temperature while the present data indicate that the number of teeth in the sex-comb of Bar varies directly with increased temperature. Furthermore, LUCE (1931) has shown that Bar is dominant in determining the direction of the change in the facet count in response to temperature while it is seen that in the Bar-infrabar stock it is the infrabar gene which dominates the temperature reaction of the development of the sex-comb.

TABLE I

	C°	MEAN TEETH (x)	MEAN TARSUS* (y)	r_{xy}	NO. OBSERVED
Bar	17°C	9.30±.03	10.71±.01	+.128±.04	340
	27°C	9.80±.04	10.00±.01	+.157±.04	333
Wild	17°C	9.80±.04	10.95±.02	+.160±.04	369
	27°C	10.23±.04	10.11±.02	+.102±.04	320
Vestigial	17°C	10.51±.05	10.07±.02	+.128±.05	216
	27°C	11.08±.04	9.25±.03	+.134±.04	251
Infrabar	17°C	12.07±.10			42
	27°C	11.39±.08			36
Bar-infrabar	17°C	11.02±.09	10.71±.04	+.214±.09	49
	27°C	10.63±.10	9.65±.03	+.613±.06	49
Double infrabar	17°C	10.52±.09			31
	27°C	9.88±.11			25

* The tarsus length is expressed in units, one of which is equivalent to .0055 mm.

DISCUSSION

Temperature studies of Drosophila have shown that some structures are increased in their development with increased temperature while others are decreased by the same temperature stimulus. Reference has already been made to the Bar and infrabar studies of eye facet counts. STANLEY (1931, 1935) and HARNLY (1930, 1936) have shown that increased temperature causes a direct variation in wing length in vestigial. The author (1934) has pointed out that the surface area of the wild type wing varies inversely with increased temperature. ANDERSON (1931) has found that within the same individual the number of rows of acrostical hairs varies directly while the facet count of Bar eyes varies inversely with increased temperature.

In the present investigation it has been shown that the number of teeth in the sex-comb varies directly with increased temperature in Bar, wild, and vestigial, and inversely with increased temperature in infrabar, Bar-infrabar, and double infrabar. It is further shown that the length of the tarsus varies inversely with increased temperature whether the infrabar

gene was present or not. These facts lead one to the conclusion that the tarsal length is not secondarily affected by the Bar series to an appreciable extent. The apparent high positive correlation of this measurement with the number of teeth in the sex-comb is coincidental since there is probably a positive correlation in the other stocks also.

It is impossible to say from the data at hand just what mechanism operates to produce these interesting results in the Bar allelomorphs. Further investigation in which a correlation of the eye facet count and the teeth in the sex-comb will be necessary to establish the hypothesis of the multiple effects of these genes upon the two characters. Another approach to the problem will be through independent selection for sex-combs and eye facets and the observation of any correlated changes in the selected and the unselected character. Since the sex-combs are modified macrochaetes and have anatomical features in common with the acrostical hairs, it will be interesting to observe the correlated effects of the bar allelomorphs on these characters in their response to temperature.

SUMMARY

1. The range of population size within which flies can be raised without reducing the tarsus length and the number of teeth in the sex-comb was determined.

2. The size of the tarsus was found to vary inversely with increase in the temperature at which the animals developed, and the number of teeth in the sex-comb was found to vary directly with increased temperature in Bar, wild and vestigial and inversely in infrabar, Bar-infrabar, and double infrabar.

3. The coefficients of correlation for the number of teeth in the sex-comb and the length of the tarsus of the same side was determined for four stocks.

4. The coefficient of correlation of the length of the tarsus of the right side with the length of tarsus on the left side was found to be $+.554 \pm .03$ and the coefficient of correlation of the number of teeth in the sex-combs of the two sides was $+.205 \pm .04$.

5. Two unusual types of sex-combs are described.

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TRANSPLANTATION OF WILD TYPE AND VERMILION EYE DISKS AMONG FOUR SPECIES OF DROSOPHILA

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INTRODUCTION

THE imaginal disk transplantation experiments of EPHRUSSI and BEADLE (1936 and 1937) and BEADLE and EPHRUSSI (1936 and 1937) offer data of great interest in the consideration of diverse problems dealing with the activity of specific genes during development. Up to the present time, their published work has dealt largely with the differentiation of eye pigments in the one species *Drosophila melanogaster*. From the results obtained, they have been led to postulate certain diffusible substances on the presence or absence of which during development the phenotypic result depends. These substances, successive products in a chain reaction in the order $ca^+ \rightarrow v^+ \rightarrow cn^+$, are essential to the production of a wild type eye. The mutation v^+ into v has apparently resulted in the deficiency or loss of both v^+ and cn^+ substances. However, the pigmentation of a genetically v eye may be modified to + by transplanting it into hosts (for example, +, *cn*, *bri*, *mah*) which are capable of completely making up this loss, or to an intermediate color by transplantation into others (*car*, g^2) also capable of furnishing the essential substances but to a lesser degree.

The present work was undertaken to determine whether the relationship between vermilion and wild type pigmentation shown to exist in *D. melanogaster* also holds within and between related species. (See also HOWLAND and GLANCY 1937.) The four species chosen were *D. melanogaster*, *D. simulans*, *D. pseudoobscura* and *D. virilis*. Among these, hybridization tests of the homology of various genes are possible only between *melanogaster* and *simulans*. Such experimental crossing has already shown the *v* gene in *simulans* to be a homologue of that in *melanogaster*. In *pseudoobscura* and *virilis* the chief genetic evidence of homology is that the *v* gene is sex-linked and has the same locus in relation to certain mutually possessed genes (METZ, MOSES and MASON 1923). The behavior of *v* on transplantation, therefore, should aid in answering this question of gene homology in the species where hybridization tests are impossible.

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MATERIALS AND METHODS

The implantations were carried out as follows: (a) one operator performing the entire routine quite independently (HOWLAND, SONNENBLICK and GLANCY 1937) or (b) two operators, one excising disks and preparing hosts, the other injecting and transferring operated animals into food vials. The second of these methods obviously is the more expeditious. The fluid (BĚLAŘ 1929) into which the disks were released from the donor and which served as a medium for injection was, in salt content, comparable to that used by EPHRUSSI and BEADLE (1936) but contained in addition a small amount of dextrose (20 cc of 9 percent NaCl, 4 cc of 1 percent KCl, 4 cc of 1 percent anhydrous $CaCl_2$, 5–10 cc of 10 percent dextrose, 0.4 cc of 10 percent $NaHCO_3$, the whole diluted to 200 cc).

The lumen of the pipette used was constricted at a suitable distance from the elliptical opening by momentary heating in a horizontal microflame (EPHRUSSI and BEADLE 1936). It was found that pipettes with sharp puncturing points and smooth edges could be prepared for use without honing. This was accomplished by crushing the capillary with a thin microknife laid obliquely across the tip at the desired angle. A thin-walled capillary more often gives a "clean" break (not jagged) and also furnishes a better cutting edge.

The stocks of *D. simulans* (+ and *v*) and *D. pseudoobscura* (+ and *y sn v*) were obtained from Pasadena, and of *D. virilis* (+ and v^3mt^3) from Cold Spring Harbor. The *D. melanogaster* stocks (Woodbury strain of + and v^2) were available at Washington Square College. The flies were allowed to lay on banana-agar in half pint bottles for a period of eight hours if about 25 females were present. To secure large and vigorous larvae for operation, small amounts of crumbled yeast were added from time to time as the larvae required it, especially large amounts being given to *D. virilis*. Vials for operated larvae were prepared with banana-agar slants sparingly seeded with dry yeast.

Since in the species used development at the same temperature proceeds at different rates, a "standard stage" of hosts and donors was arbitrarily chosen, that is, approximately 24 hours before puparium formation. The difficulty in choosing exactly similar stages is apparent. A valuable check on the stage used is the degree of development of the donor disk. By also noting the condition of other disks, especially the wing-thoracic in which a rapid series of visible changes occurs at this period, the stage can be more precisely judged.

The temperatures at which the experiments were carried on were varied at different times during the course of the work, but as a control measure both stock and operated animals were always kept at the same temperature. When *D. melanogaster*, *D. simulans* and *D. virilis* were used, the

temperature range was from 23° to 25°C. Since the *D. pseudoobscura* stock is more vigorous at about 19°C (DOBZHANSKY 1935), when using this species as hosts, they were in some instances kept at this temperature.

Since even the pigmentation of a self-implant differs from that of the inner surface of the host eye, control implants (*v* in *v*, + in +) were used for color comparison. Implants were dissected in absolute alcohol, a medium in which the eye color is not altered for several hours. The adoption of a standard background and lighting unit was found to be highly essential. All implants were examined against a black unglazed background, in the direct light from a Spencer projection lamp equipped with a Mazda 100 watt projection bulb.

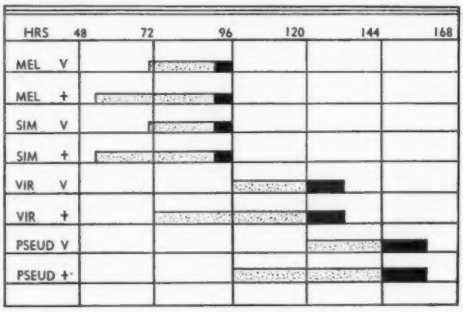

FIGURE 1. Composite diagram, based on data derived from SCHULTZ, STURTEVANT, GLANCY, COCHRANE and POULSON, to show the relative time of pigment deposition in the vermilion and wild type eyes of the four species used. Though no end point for this process is given by SCHULTZ, it is a matter of common observation that this is reached some hours before eclosion. The duration of the pupal period and the time of pigment formation in *D. simulans* have been represented as the same as that in *D. melanogaster* since STURTEVANT states that the life cycles are approximately the same in these two species. The numbers 48–168 signify hours after puparium formation. Stippled blocks represent the period of pigment deposition; solid blocks, the time elapsing before eclosion.

LENGTH OF LIFE CYCLE AND EYE COLOR DEVELOPMENT

An approximate knowledge of the length of the developmental cycle in the four species used is essential in choosing hosts and donors of "standard" age and also serves as a basis for interpreting the experimental data to follow. The length of the life cycle (at 25°C) of the various species used has been determined by different investigators. As is well known, the time required for development of wild type *melanogaster* at this temperature is about nine days. This time may be divided into three periods: the egg period, slightly less than one day; larval period, about four days; and pupal period, also about four days, (BONNIER 1926; POWSNER 1935). Essentially the same figures apply to *simulans* (STURTEVANT 1929). *Dro-*

sophila pseudoobscura develops much more slowly. Accurate data for different races are given by POULSON (1934). The approximate figures for the race used (Texas A) are: egg-larval period 6½ days, pupal period 6½ days. The data for *virilis* as observed in this laboratory by E. A. GLANCY, are as follows: egg period 1⅓ days, larval period 5½ days, and pupal period also 5½ days. In all these species, the females develop somewhat more rapidly than the males, so there is a difference of several hours in the total period. This discrepancy in rates is accentuated in the more slowly developing forms and in *pseudoobscura* amounts to 8–13 hours on the average. The rate of development of the vermilion mutant does not differ significantly from that of the wild type in any of the species used.

The time of coloration of the eye has been determined for the wild type and vermilion of *melanogaster* (SCHULTZ 1935), for *pseudoobscura* (COCHRANE 1936), and for *virilis* (GLANCY, unpublished). These data are summarized in figure 1. In all species observed, the wild type differs from the vermilion mutant by the earlier deposition of pigments; first pale yellow, next tan, and subsequently red. Then both the vermilion eye, which has up to now been colorless, and the wild type eye simultaneously lay down two pigments, red and yellow. The *v* eye then differs from + mainly in the omission of the preliminary stages of pigment deposition.

EXPERIMENTAL DATA

Implants of + and v eye disks from D. melanogaster

Interspecific transplantation of wild type and vermilion optic disks of *melanogaster* gives results identical with those of EPHRUSSI and BEADLE (1935) for *melanogaster* alone. The data are embodied in table 1. When both hosts and donors used are of "standard" age, the wild type disks of *melanogaster* develop autonomously[1] in the wild type and vermilion hosts of all species. The vermilion eye disks, as would be expected, remain vermilion on implantation into vermilion hosts of any of the species used, but are modified to wild type when transferred to wild type hosts. Inter-

[1] The + implants of *D. melanogaster*, *D. simulans* and *D. pseudoobscura* do not differ appreciably in color if perfect implants are examined whole. This is especially true of the + implants of *melanogaster* and *simulans*, the color range in + *pseudoobscura* implants showing a greater variability. If, however, the colored layers be lifted off from the chitin, the inner surface of the implant (outer layer of the eye) is seen to be a brownish yellow in *pseudoobscura* and a light yellowish color in both *simulans* and *melanogaster*. By such a test, *pseudoobscura* implants may be set off from *melanogaster* and *simulans*, but the latter two still offer no critical point of contrast. It is with these reservations in mind that the implant phenotypes of these three species are designated as autonomous. On critical comparison of the color of the vermilion eyes in flies (24 hours old) of the four species, a slight difference is observed in the amount of red pigment present, *melanogaster* (v^2) and *simulans* (v) having the least, *pseudoobscura* (v) slightly more, and *virilis* (v^3) the greatest amount. This variation was not noted uniformly in all of the implants, but, as nearly as could be determined without recourse to other timing methods, the different vermilions were autonomous when implanted in vermilion.

mediate colors have been obtained by transplanting a young + eye disk into an older *v* host (BEADLE and EPHRUSSI 1936, and EPHRUSSI and BEADLE 1937). This is true also in interspecific transplantations. All the above results hold regardless of sex.

Implants of + and v eye disks from D. simulans

In *D. simulans*, the behavior of both + and *v* eye disks on implantation in + and *v* hosts of all four species is the same as that of disks of *D. melanogaster* (95 implants observed). It is impossible to distinguish between the color of *simulans* and *melanogaster* eyes of the same phenotype, in either implant or fly.

TABLE 1

Implants of + and v^2 eye disks from D. melanogaster.

IMPLANT	HOST	PHENOTYPE OF IMPLANT*	NUMBER OF IMPLANTS
(from *D. mel.*)			
+	*D. mel.*+	*D. mel.* +	9
+	*D. sim.* +	*D. mel.* +	10
+	*D. pseud.* +	*D. mel.* +	5
+	*D. vir.* +	*D. mel.* +	4
+	*D. mel.* v^2	*D. mel.* +	4
+	*D. sim. v*	*D. mel.* +	7
		Intermediate	1 (donor young)
+	*D. pseud. v*	*D. mel.* +	16
+	*D. vir.* v^3	*D. mel.* +	3
v^2	*D. mel.* +	*D. mel.* +	11
v^2	*D. sim.* +	*D. mel.* +	7
v^2	*D. pseud.* +	*D. mel.* +	4
v^2	*D. vir.* +	*D. mel.* +	7
v^2	*D. mel.* v^2	*D. mel.* v^2	3
v^2	*D. sim. v*	*D. mel.* v^2	17
v^2	*D. pseud. v*	*D. mel.* v^2	2
v^2	*D. vir.* v^3	*D. mel.* v^2	3

* See footnote 1.

Implants of + and v eye disks from D. pseudoobscura

The results obtained on implantation of + and *v* optic disks of *D. pseudoobscura* within and between the four species are essentially the same as those just reported for *melanogaster* and *simulans* (113 implants observed). Since the life cycle of this species (see section on life cycles) is significantly longer than that of *melanogaster* and *simulans*, it was to be expected that intermediate stages in pigmentation development or even colorless stages might occur. The records show that 13 such implants were intermediate in color. Both + and *v* disks in hosts of both types give intermediates. (See discussion.)

The autonomous development of the yellow body color in these implants had to be taken into consideration when examining them. The yellow chitinous layer of the *y sn v* eye contrasted sharply with the darker chitin of the + body color.

Implants of + and v eye disks from D. virilis

Auto-implantation of + optic disks in *D. virilis* leads to the production of a color which resembles Rose Red (RIDGWAY, Plate XII) more than

TABLE 2

Implants of + and v eye disks from D. virilis.

IMPLANT	HOST	PHENOTYPE OF IMPLANT*	NUMBER OF IMPLANTS*
(from *D. virilis*)			
+	*D. mel.* +	*D. vir.* +	6
+	*D. sim.* +	*D. vir.* +	1
+	*D. pseudo.* +	*D. vir.* +	6
+	*D. vir.* +	*D. vir.* +	5
+	*D. mel.* v^2	*D. vir.* +	6
+	*D. sim. v*	*D. vir.* +	18
		Intermediate	13(donors young)
+	*D. pseudo. v*	*D. vir.* +	7
+	*D. vir.* v^3	*D. vir.* +	8
v^3	*D. mel.* +	*D. mel. sim.* or *pseudo.* +	3
		Intermediate	4
v^3	*D. sim.* +	*D. mel. sim.* or *pseudo.* +	2
v^3	*D. pseudo.* +	*D. mel. sim.* or *pseudo.* +	13
v^3	*D. vir.* +	*D. mel. sim.* or *pseudo.* +	60
v^3	*D. mel.* v^2	*D. vir.* v^3	3
v^3	*D. sim. v*	*D. vir.* v^3	3
v^3	*D. pseudo. v*	*D. vir.* v^3	4
v^3	*D. vir.* v^3	*D. vir.* v^3	2

* See footnote 1.

the + color of *melanogaster, simulans* or *pseudoobscura* (Compare Nopal Red, RIDGWAY, Plate I). This same pigmentation is obtained on implantation of *virilis* + eye disks into the + and *v* hosts of the other three species. (Table 2). The vermilion (v^3) eye disk, as expected, develops autonomously in the *v* host of every species used. In a + host, vermilion is modified to the same color as is the *v* disk of any of the other species, that is, to wild type. Never is it modified to the + of *virilis*, but always to the color of the + implants of the other species. No other vermilion is modified to "Rose Red."

In making implants of *virilis* v^3 eye disks in + hosts of the same species, the age of both host and donor was varied. Eye disks from v^3 larvae 2-2½ days before puparium formation were transplanted into + hosts of the same age and also into + hosts twenty-four hours older. Varying the age of host and donor in this way did not modify the results to any great extent.

As the pupal period of *virilis* is approximately one and a half days longer than that of *melanogaster* and *simulans*, it might be expected that optic disks from *virilis* implanted into these shorter-cycle animals would not have reached their full pigmentation at the time of hatching of the fly. Intermediate colors are, therefore, to be expected. They were sometimes obtained.

DISCUSSION

Interest in the data offered by interspecific eye disk transplantation centers chiefly in the new evidence for the homology of the vermilion gene in *D. melanogaster*, *D. simulans*, *D. pseudoobscura* and *D. virilis*. The already available information supporting this contention rests (1) on hybridization experiments between *melanogaster* and *simulans* and (2) on the similar sequence of loci common to the species concerned. In the latter case, however, although there are a few sex-linked genes which have the same locus relative to vermilion, others are not so placed (METZ, MOSES and MASON 1923).

Assuming that the vermilion gene is homologous in all four species its behavior would be expected to parallel that of the vermilion gene in *melanogaster*. In other words, a *v* eye disk, when implanted in a + host, should be modified to + through the activity of the v^+ and cn^+ substances, (progressively formed products in the chain reaction $ca^+ \rightarrow v^+ \rightarrow cn^+$) necessary for the formation of the + phenotype (BEADLE and EPHRUSSI 1936). Since this is essentially true the presence of the last two substances in all four species is definitely established. However, the results obtained on implantation of *virilis* v^3 in its own + host are slightly at variance with those obtained with the vermilion of the other three species in their wild type hosts. It must be recalled, however, that the implantation of the *virilis* v^3 eye disks in either the + or the *v* hosts of all four species leads to the production of an eye color which, superficially at least, is the same as that given by the *v* disk of any of the other three species. In this respect the behavior of v^3 in *virilis* is identical with that of the *v* of *melanogaster*, *simulans*, and *pseudoobscura*. The difference lies in the relationship of v^3 to its own + allele which on implantation is of a darker color than the + of *melanogaster*. With respect to its own +, this vermilion of *virilis* is intermediate, while with respect to the + of the other species it is com-

pletely modified to +. It may be that another allele of v^3 will more nearly approach the color of the + implant of *virilis* on implantation into *virilis* +. An additional reaction may be involved in producing the + pigmentation of *virilis*, or some modifying genes may be present in this stock.

Although *pseudoobscura* and *virilis* have much slower growth rates than *melanogaster* and *simulans* (fig. 1), implants of *v* disks from long-cycle donors into short-cycle hosts frequently attained complete pigmentation. This was especially surprising in a cross implant such as *pseudoobscura v* (which at 25°C develops color 120 hours after puparium formation, COCHRANE 1936) into *melanogaster* + or *v* which at 25°C has a pupal period of about 96 hours (POWSNER 1935). The expectation would be a colorless implant on hatching of the host fly, but none was ever found. To account for these discrepancies, the following suggestions are offered. Injury of the host larva (but not the disk) which in almost all cases noticeably extends the period of pupation, may allow the disk sufficient time to lay down pigment before emergence of the imago. Further, the great difficulty attendant upon consistent selection of host and donor larvae of identical stages of development may lead to the choice of organisms varying somewhat in stage. It is also possible that the rate of development of a short-cycle host may accelerate the rate of pigment deposition in the long-cycle donor disk.

SUMMARY

1. Transplants of vermilion and wild type optic disks of mature larvae have been made within and between four species of Drosophila, namely, *D. melanogaster*, *D. simulans*, *D. pseudoobscura* and *D. virilis*. The results obtained are essentially the same as those of BEADLE and EPHRUSSI on *D. melanogaster*, showing that the action and occurrence of the v^+ and cn^+ substances postulated by them are not restricted to a single species. This supplies additional evidence for the homology of the vermilion gene in all four species.

2. Wild type disks of each of these species develop autonomously in wild type and vermilion hosts of all four species. The pigmentation of the wild type implants, as determined by gross observation (5), is the same for the first three named, but is always darker in *virilis* implants in every host.

3. Vermilion disks of all species studied remain vermilion in a vermilion host of any one of these species.

4. Vermilion disks on implantation to wild type hosts are modified to wild type. This is true of vermilion disks of all four species allowed to develop in wild type hosts of every species used. In a *virilis* wild type host, the phenotype of the *v* implant of all species used including *virilis* v^3 is

not that of *virilis* + control implants. It more closely resembles the color of the + implants of the other species.

5. Intermediate stages in pigmentation are often obtained when a disk from a long-cycle donor (*pseudoobscura*, *virilis*) has been transplanted to a short-cycle host (*melanogaster*, *simulans*).

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INHERITANCE IN BARLEY II

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INTRODUCTION

CHLOROPHYLL deficient seedlings are rather common in cultivated barleys. While the plants themselves are of little value economically, their use in linkage studies is important. The location of characters of economic importance in the various linkage groups is necessary for a thorough understanding of breeding problems in barley. The present studies involve the locating of the factors for three different chlorophyll deficiencies in two of the seven linkage groups in barley.

REVIEW OF LITERATURE

The review of literature on the linkage groups in barley is confined to the characters studied in this paper.

Chlorophyll deficiencies. Several factors for chlorophyll deficiencies are already located in the various linkage groups. Trebi I (ROBERTSON 1929) contains $A_t a_t$ (green versus white seedlings). This pair is linked with black and white glume color and is in Group II. Minnesota 84–7 (ROBERTSON et al, 1932) is a chlorina plant carrying *ff* in Group I. Colsess I (ROBERTSON 1929) carries $A_c a_c$ (green versus white seedlings). Colsess IV (ROBERTSON 1929) carries $X_c x_c$ (green versus zantha seedlings). Both $A_c a_c$ and $X_c x_c$ are in Group VI. Colsess V (ROBERTSON and DEMING 1930) is a chlorina plant carrying $f_c f_c$. Coast III (ROBERTSON and DEMING 1930) carries $Y_c y_c$ (green versus virescent seedlings). Both $F_c f_c$ and $Y_c y_c$ are in Group VII.

Interaction of other characters. A review of the inheritance of the following factor pairs is given by DAANE (1931): six-row versus non-six-row, black versus white glume color, covered versus naked caryopsis, hooded versus awned, long versus short-haired rachilla, and rough versus smooth awned. He also discusses the reaction of the intermedium versus non-intermedium factor pair, *Ii*, with the six-row versus non-six-row character.

Linkage groups. The following factor pairs used in this study have been placed in linkage groups by KUCKUCK (1930), DAANE (1931), and ROBERTSON (1932, 1933): Group I—*Vv* for six-row versus non-six-row; Group II—*Bb*, black versus white glume color; Group III—*Nn*, covered versus naked caryopsis; and Group IV—*Kk*, hooded versus awned. KUCKUCK suggests that the linkage of Albino-4, Chlorina and Albino-3 described by NILSSON-EHLE and HALLQUIST may form a fifth group. However, the investigations of ROBERTSON et al (1932) indicate that this linkage series belongs to

Group I. DAANE and ROBERTSON et al place *Rr* (rough versus smooth awn) and *Ss* (long versus short-haired rachilla) in Group V. ROBERTSON et al place A_cA_c and X_cX_c in Group VI. Group VII (ROBERTSON 1933) contains the Colsess V chlorina factor pair F_cF_c and the factor pair Y_cY_c for green versus virescent found in Coast III.

MATERIALS AND METHODS

This paper discusses the inheritance of three chlorophyll deficient seedling factor pairs and their interactions with the following factor pairs.

Linkage Group	*Character Pair*	*Symbols*
I	Non-six-row versus six-row	*Vv*
	Green versus chlorina	*Ff*
II	Black versus white glume color	*Bb*
	Green versus white seedlings	A_tA_t
III	Covered versus naked caryopsis	*Nn*
IV	Hooded versus awned	*Kk*
	Intermedium versus non-intermedium	*Ii*
V	Rough versus smooth awn	*Rr*
	Long versus short haired rachilla	*Ss*
VI	Green versus white seedlings	A_cA_c
	Green versus zantha seedlings	X_cX_c
VII	Green versus chlorina seedlings	F_cF_c
	Green versus virescent seedlings	Y_cY_c

The parental varieties used were Coast II, *H. dis. nigrinudum* I, and Smyrna I, differentiated by the factor pairs enumerated in table 1.

TABLE 1

Factor pairs found in the different parents.

COAST II	H. DIS. NIGRINUDUM I	SMYRNA I
vv	*VV*	*VV*
FF	*FF*	*FF*
bb	*BB*	*bb*
A_tA_t	A_tA_t	A_tA_t
NN	*nn*	*NN*
kk	*kk*	*kk*
II	*II*	*ii*
ss	*ss*	*SS*
RR	*RR*	*RR*
A_cA_c	A_cA_c	A_cA_c
X_cX_c	X_cX_c	
F_cF_c	F_cF_c	F_cF_c
$A_{c2}a_{c2}$	$A_{c2}A_{c2}$	X_cx_c
	Y_cY_c	
	A_na_n	

Coast II, described by ROBERTSON and DEMING (1932), contains the pair, $A_{c2}a_{c2}$, (green versus white seedlings). *H. dis. nigrinudum* I is a selection from the original strain of *H. dis nigrinudum* (HARLAN 1918) and is heterozygous for green versus white seedlings. The segregation of the seedling character shows a 3:1 ratio, indicating that the chlorophyll deficient seedling is caused by the interaction of a single factor pair A_na_n. Smyrna I is a selection from Smyrna which is heterozygous for yellow seedling X_sx_s. It segregates into a 3:1 ratio of green and yellow seedlings, indicating that a single factor pair is responsible. Table 2 gives data showing the F_2 segregation of green versus chlorophyll deficient seedlings in *H. dis. nigrinudum* and Smyrna I.

TABLE 2

Seedling counts of families heterozygous for chlorophyll deficient seedlings.

VARIETY	GREEN	CHLOROPHYLL DEFICIENT	D/P. E.
H. dis. nigrinudum I	3240	1056	0.94
Smyrna I	936	342	2.16

Methods similar to those described in a previous publication (ROBERTSON 1929) were used.

INTERACTION OF SIMPLE MENDELIAN FACTOR PAIRS

Group I. The factor pairs $A_{c2}a_{c2}$, A_na_n and X_sx_s were studied in their relationship to the factor pairs *Vv* and *Ff* located in Group I. The factors showing independent inheritance are given in tables 3 and 4.

A good fit, table 3, is obtained to a calculated 9:3:4 ratio for both white seedling factor pairs and non-six-row versus six-row. The yellow seedling factor pair X_sx_s in Smyrna I, however, shows a poor fit to a 9:3:4 ratio obtained with independent inheritance of the factor pairs *Vv* and X_sx_s. The non-six-row factor pair went into the cross with the heterozygous lethal and if linkage occurs this class should be low, which is the case. A further check was made in F_3 and the data from this test are presented in table 4.

The genetic constitution as determined by the F_3 segregation does not indicate linkage. The above result shows that X_sx_s is inherited independently of *Vv*.

Interactions of $A_{c2}a_{c2}$, A_na_n and X_sx_s were studied with *Ff* in Group I. Minnesota 84–7 homozygous for *ff* was crossed with Coast II, *H. dis. nigrinudum* I and Smyrna I. The F_2 seedling counts for the various crosses studied are given in table 3.

The cross involving *H. dis. nigrinudum* I×Minnesota 84–7 fits the calculated 9:3:4 ratio very well, indicating independence of A_na_n and *Ff*.

The other two crosses give poor fits to the calculated 9:3:4 ratio. The genetic constitution of the F_2 plants was again determined from the F_3 plant behavior (table 4).

TABLE 3

F_2 segregation of factor pairs showing independent inheritance.

CROSS	GENOTYPES STUDIED	GROUP	PHENOTYPES			χ^2	P
			AB*	aB	Ab and ab		
Coast II×*H. dis. nigrinudum*	*Vv* $A_{c2}a_{c2}$	I	492	151	209	0.89	Very large
Coast II×Minn. 84–7	*Ff* $A_{c2}a_{c2}$	I	1398	546	646	9.89	0.0072
Coast II×*H. dis. nigrinudum*	*Bb* $A_{c2}a_{c2}$	II	478	181	207	2.72	0.2633
Coast II×Colsess IV	*Kk* $A_{c2}a_{c2}$	IV	1362	489	656	3.78	0.1551
H. dis. nigrinudum I×Coast III	*Vv* A_na_n	I	557	166	220	3.04	0.2194
H. dis. nigrinudum I×Minn. 84–7	*Ff* A_na_n	I	419	163	175	4.31	0.1190
H. dis. nigrinudum I×Coast III	*Bb* A_na_n	II	534	188	219	1.92	0.3866
H. dis. nigrinudum I×Coast III / *H. dis. nigrinudum* I×Smyrna I	*Nn* A_na_n	III	551	206	230	3.54	0.1759
H. dis nigrinudum I×Colsess IV	*Kk* A_na_n	IV	1023	376	470	2.64	0.2748
H. dis. nigrinudum I×Smyrna I	*Ss* A_na_n	V	583	198	241	1.15	0.5707
H. dis. nigrinudum×Colsess V	F_cf_c A_na_n	VII	730	215	321	2.62	0.2777
Smyrna I×Coast III	*Vv* X_sx_s	I	710	284	348	7.30	0.0266
Smyrna I×Minn. 84–7	*Ff* X_sx_s	I	510	219	221	11.64	0.0031
Smyrna I×*H. dis. nigrinudum*	*Bb* X_sx_s	II	241	103	119	4.56	0.1054
Smyrna I×*H. dis. nigrinudum*	*Nn* X_sx_s	III	2083	704	986	2.68	0.2691
Smyrna I×Colsess I	*Kk* X_sx_s	IV	724	205	342	6.62	0.0376
Smyrna I×Colsess	*Ii* X_sx_s	IV	452	189	234	8.14	0.0173
Smyrna I×Colsess	*Ss* X_sx_s	V	874	282	424	3.06	0.2179
Smyrna I×Colsess V	F_cf_c X_sx_s	VII	1365	442	653	3.41	0.1875
Smyrna I×Coast III	Y_cy_c X_sx_s	VII	359	141	150	4.08	0.1310

* AB represents the double dominant class.

aB represents the class containing a viable recessive class.

Ab and ab represent classes containing chlorophyll deficiencies in the recessive condition. Both of these classes die in the seedling stage.

The F_3 data indicate independence of $A_{c2}a_{c2}$ and *Ff* and of A_na_n and *Ff*. The data showing the interaction of the linked factor pairs *Vv* and *Ff* in

TABLE 4

F_2 genotypes as determined by F_3 segregating families from the double dominant plants in F_2.

CROSS	GENOTYPES STUDIED	GROUP	GENOTYPES				χ^2	P
			AABB	AABb	AaBB	AaBb		
Smyrna I×Coast III	*Vv* X_sx_s	I	92	222	199	454	4.99	0.1723
Coast II×Minn. 84–7	*Ff* $A_{c2}a_{c2}$	I	64	144	133	249	2.00	0.5728
Smyrna I×Minn. 84–7	*Ff* X_sx_s	I	38	83	94	144	4.27	0.2373
Coast II×Trebi I	A_{s1} $A_{c2}a_{c2}$	II	143	515		568	2.96	0.2293
Smyrna I×Colsess I	*Kk* X_sx_s	IV	72	145	176	292	4.79	0.1908
Smyrna I×Colsess	*Ii* X_sx_s	IV	57	94	108	193	2.21	0.5348
Smyrna I×Colsess V	F_cf_c X_sx_s	VII	61	237		279	3.61	0.1698
H. dis. nigrinudum I×Colsess V	F_cf_c A_na_n	VII	72	156	151	351	4.21	0.2426
H. dis. nigrinudum I×Coast III	Y_cy_c A_na_n	VII	23	37	40	83	0.73	Very large

Group I with the factors for the various chlorophyll deficiencies $A_{c2}a_{c2}$ found in Coast II, A_na_n found in *H. dis. nigrinudum* I, and X_sx_s found in Smyrna I indicate that they are inherited independently.

Group II. The factor pairs *Bb* for black versus white glume color and $A_t a_t$ for green versus white seedlings (Trebi I) have previously been located in Group II. The interaction of the factor pair *Bb* for black versus white glumes and the three seedling lethals are given in table 3.

All of the observed ratios give a good fit to a calculated 9:3:4 ratio indicating that the chlorophyll deficient factor pairs react independently of *Bb*.

A further test for linkage in Group II was determined from the reaction of green versus white seedlings in Coast II and green versus white seedlings in Trebi I. The F_2 segregation of green and white seedlings approached a 9:7 ratio, indicating that $A_{c2}a_{c2}$ and $A_t a_t$ were inherited independently of each other. Further proof of independence was found from the F_2 genetic constitution as determined by F_3 seedling counts from the F_2 green plants (table 4).

Group III. So far only one factor pair *Nn* has been located in Group III. Crosses were made involving the interaction of *Nn* for covered versus naked seeds and the three chlorophyll deficient factor pairs.

The F_2 data (table 3) from the crosses involving $A_n a_n$, $X_s x_s$, and *Nn* show a good fit to the 9:3:4 ratio, indicating independent inheritance. The cross involving $A_{c2}a_{c2}$ and *Nn* do not fit the calculated 9:3:4 ratio (table 5). The covered class is low in numbers while the naked class is high. This indicates linkage since covered went into the cross with the seedling defect.

In order to test the possibility of linkage of $A_{c2}a_{c2}$ and *Nn*, an F_3 generation was grown and the F_2 genotypes determined. From the data obtained, a crossover percentage was determined by the use of IMMER'S (1934) formulae for F_2 and F_3 data. The best fit for both F_2 and F_3 data was obtained with a crossover percentage of 27.24 ± 2.04.

Both the F_2 phenotypes and genotypes fit a calculated ratio with 27.24 percent crossing over, indicating linkage of $A_{c2}a_{c2}$ and *Nn*.

Group IV. The factor pairs *Kk* and *Ii* are located in Group IV. The interactions $A_{c2}a_{c2}$, $A_n a_n$, $X_s x_s$ and *Kk* were tested. The F_2 segregations are given in table 3. The data indicate that *Kk* is inherited independently of $A_{c2}a_{c2}$ in Coast II and $A_n a_n$ in *nigrinudum* I. However, there is a poor fit to the 9:3:4 ratio for *Kk* and $X_s x_s$.

The genetic constitution of the F_2 plants as determined from F_3 segregations indicates a slightly better fit (table 4).

A further test was made to determine the interaction of the chlorophyll deficient factor pairs with *Ii* which is linked with *Kk*, the crossover value value being 15.12 ± 0.065 percent.

The six-row plants were dropped since it is impossible to determine *Ii* where *vv* is present. Since the six-row green plants were not used a correction was made to account for the six-row genotypes in the yellow seedlings.

TABLE 5

Fit of the F_2 phenotypes and F_2 genotypes to 9:3:4 and 1:2:2:4 ratios and to calculated ratios with 27.24 percent crossing over.

F_2 PHENOTYPES	GREEN COVERED	GREEN NAKED	WHITE COVERED AND NAKED	χ^2	P
Observed ratio	448	210	215		
Calculated 9:3:4 ratio	491.06	163.69	218.25	16.93	0.0002
Calculated ratio with 27.24 percent crossing over	452.69	202.06	218.25	0.4090	Very large

F_2 GENOTYPES	$A_{c2}A_{c2}$ *NN*	$A_{c2}A_{c2}$ *Nn*	$A_{c2}a_{c2}$ *NN*	$A_{c2}a_{c2}$ *Nn*	χ^2	P
Observed ratio	16	86	85	257		
Calculated 1:2:2:4	49.33	98.67	98.67	197.33	44.08	Very small
Calculated ratio with 27.24 percent crossing over	15.88	84.85	84.85	258.42	0.0246	Very large

The observed segregation fits the 9:3:4 calculated ratio very poorly. The F_2 genotypes were determined from the F_3 families (table 4) and a good fit to a calculated 1:2:2:4 ratio was obtained indicating independent inheritance for *Ii* and X_sx_s.

Group V contains *Rr* (rough versus smooth awn) and *Ss* (long versus short haired rachillas). The interaction of *Ss* was tested in crosses of Smyrna I×Colsess and *nigrinudum*×Smyrna I.

The data in table 3 indicate that both factor pairs are inherited independently of *Ss*.

The other factor pair *Rr* in Group V was tested with X_sx_s in Smyrna I. A low number of yellow seedlings was obtained which increased the error for the third and fourth classes. These are combined because the deficient seedlings do not survive. When a correction was made from the gametic ratio to account for the missing seedlings, a good fit to the corrected 9:3:4 ratio was obtained, indicating that X_sx_s is not in the fifth linkage group.

Group VI contains the two chlorophyll deficient seedling factor pairs A_ca_c and X_cx_c found in Colsess I and Colsess IV, respectively. They are linked with less than 4 percent crossing over.

The interaction of the Coast II factor pair $A_{c2}a_{c2}$ was found to be independent of X_cx_c, ROBERTSON and DEMING (1932). The interaction of the other two pairs A_na_n and X_sx_s were tested in crosses between Smyrna I and Colsess I and between *H. dis. nigrinudum* I and Colsess IV. Neither of the observed ratios fit the calculated 9:3:4 ratio (table 6). The F_2 genotypes were determined from the F_3 seedling behavior and the data are presented in table 6. The data show a poor fit to a calculated 1:2:2:4 ratio when tested for independent inheritance.

A possible linkage is indicated by the F_2 and F_3 data. Calculations of the crossover value which would best fit the F_2 and F_3 data were made by the use of the IMMER formula. The best fit (table 6) of the F_2 and F_3 data

TABLE 6

Fit of the F_2 phenotypes and F_2 genotypes to a calculated 9:3:4 and 1:2:2:4 ratio and to a calculated ratio with 25.74 and 9.37 percent crossing over.

CROSS	CALCULATED RATIO	OBSERVED PHENOTYPES F_2			χ^2	P
		GREEN	YELLOW	WHITE		
Smyrna I×Colsess I	9:3:4	567	268	263	23.37	Very small
H. dis. nigrinudum I ×Colsess IV	9:3:4	1433	560	667	10.21	0.0062
	CROSSOVER PERCENT	CALCULATED RATIO				
Smyrna I×Colsess I	25.74	567.20	256.30	274.50	1.10	0.5683
H. dis. nigrinudum I ×Colsess IV	9.37	1335.85	659.15	665.00	21.99	Very small

CROSS	CALCULATED RATIO	F_2 GAMETIC RATIO				χ^2	P
		AABB	*AABb*	*AaBB*	*AaBb*		
Smyrna I×Colsess I	1:2:2:4	14	110	110	331	67.17	Very small
H. dis. nigrinudum I ×Colsess IV	1:2:2:4	2	97	98	935	681.26	Very small
	CROSSOVER PERCENT	CALCULATED RATIO					
Smyrna I×Colsess I	25.74	18.12	104.54	104.54	337.80	1.64	0.6439
H. dis. nigrinudum I ×Colsess IV	9.37	4.96	95.68	95.68	935.68	1.84	0.6087

for the cross involving Smyrna I×Colsess I was 25.74 ± 1.73 percent of crossing over, while for the cross involving *H. dis nigrinudum* I ×Colsess IV it was 9.37 ± 0.21 percent of crossing over. The observed ratios fit the calculated gametic ratios very well, indicating linkage of the $A_c a_c$ found in Colsess I and $X_s x_s$ found in Smyrna I as well as a linkage of $X_c x_c$ in Colsess IV and $A_n a_n$ in *H. dis. nigrinudum* I.

In order to determine the linear arrangement of the genes, Smyrna I and *H. dis. nigrinudum* I were crossed and linkage values (table 7) found.

The data in the table indicate that there is linkage between $X_s x_s$ and $A_n a_n$. Since $A_n a_n$ and $X_s x_s$ are linked with $X_c x_c$ and $A_c a_c$ and since the latter are closely linked, it is evident that all four factor pairs are in the same linkage group. The arrangement on the chromosome is given below.

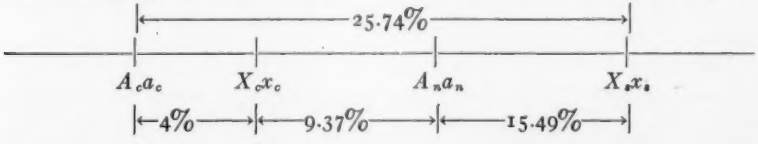

TABLE 7

Fit of the observed F_2 and F_3 data to a calculated linkage value of 15.49 ± 0.86 which gives the best fit to F_2 and F_3 data for the factor pairs $A_n a_n$ and $X_s x_s$.

	F_2 PHENOTYPES					
	GREEN	YELLOW	WHITE	χ^2	P	
Observed ratio	1186	574	574			
Calculated 15.49 percent crossover	1177.97	572.53	583.50	0.21	Very large	
	F_3 GENOTYPES					
	$X_s X_s A_n A_n$	$X_s x_s A_n A_n$	$X_s X_s A_n a_n$	$X_s x_s A_n a_n$	χ^2	P
Observed ratio	12	148	156	845		
Calculated 15.49 percent crossover	13.77	150.17	150.17	846.89	0.4894	Very large

Unfortunately, the linkage between $X_c x_c$ and $X_s x_s$ cannot be determined at present since the two yellow seedling lethals are hard to separate when segregating in the same cross.

Group VII contains $F_c f_c$ (green versus chlorina) found in Colsess V and $Y_c y_c$ (green versus virescent) found in Coast III. The interaction of $F_c f_c$ was previously reported (ROBERTSON and DEMING 1932) to be inherited independently of $A_{c2} a_{c2}$. Green versus white seedlings found in Coast II. The segregations of $F_c f_c$ and $Y_c y_c$ with $X_s x_s$ and $A_n a_n$, as given in table 3, indicate independent inheritance.

The F_2 genotypes as determined by F_3 seedling behavior further indicate this independence (table 4).

SUMMARY

Three chlorophyll deficient seedling factor pairs were tested with known factor pairs located in the seven different linkage groups in barley.

A factor pair $A_{c2} a_{c2}$ for green-versus white seedlings in Coast II was found to be linked with *Nn* (covered versus naked seeds) in Group III. The crossover percentage was 27.24 ± 2.04.

The data further indicated that $A_{c2} a_{c2}$ was inherited independently of the factor pairs located in five of the other linkage groups.

The factor pair $X_s x_s$ (green versus yellow seedlings) in Smyrna I (Citron Green, Ridgway, Plate 31) was found to be linked with factor pairs found in Group VI.

The factor pair $A_n a_n$ (green versus white seedlings) found in *H. dis. nigrinudum* I was found to be linked with $X_s x_s$ and a factor pair found in Group VI. The linkage relations were as follows: $A_c a_c$ and $X_c x_c$ linked with

less than four percent of crossing over (ROBERTSON 1929)). $X_s x_s$ linked with $A_c a_c$ with 25.74 ± 1.73 percent of crossing over, $A_n a_n$ linked with $X_c x_c$ with 9.37 ± 0.65 percent of crossing over, and $X_s x_s$ linked with $A_n a_n$ with 15.49 ± 0.86 percent of crossing over.

The linear arrangement is evidently $A_c a_c$, $X_c x_c$, $A_n a_n$ and $X_s x_s$.

The data studied indicated that $A_n a_n$ and $X_s x_s$ are inherited independently of the factor pairs located in the other linkage groups.

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INDUCTION OF DOMINANT LETHAL EFFECTS BY X-RADIATION IN HABROBRACON

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MULLER in 1927 stated that the "partial sterility" of X-rayed males of Drosophila was due, at least to an appreciable extent, to dominant lethal changes induced in the sperm. It was impossible, however, to determine whether the eggs were actually "fertilized." In Drosophila the result would be the same; the eggs would fail to develop, whether dominant lethals were induced or the sperm were inactivated so that they could not penetrate the eggs. MULLER attributed a shift in the sex ratio by reduction in the number of females to lethals in the X chromosome.

STANCATI (1932) presented evidence that dominant lethals were induced by X-radiation of sperm in Habrobracon. In this wasp in which males develop by haploid parthenogenesis, any reduction in percentage of females due to inactivation of sperm should be compensated by increase in number of male offspring, "step-sons" of the treated males. The number of "step-sons" should remain constant, however, despite the decrease in females if such decrease were due to dominant lethals alone, the number of eggs fertilized remaining constant. STANCATI's material was complicated by the presence of highly inviable biparental males which are now known to replace a variable number of females when the parents are closely related. Grouping all biparentals, males and females, together, STANCATI reported 64.8 percent of biparentals in fraternities from untreated sires, while only 24.3 percent of biparentals occurred in bisexual fraternities from treated sires. In addition to these there were 1111 sisterless males in 48 unisexual fraternities, "step-sons" of treated males. The three groups: controls, bisexual fraternities from treated and unisexual from treated males, show as average numbers of offspring per vial: 9.64, 6.16 and 4.94 respectively, indicating that decrease in biparentals is not compensated by increase in impaternate males as it is when sperm are lacking.

It has also been shown (GREB 1933 and WHITING 1935) that reduction in percentage of females occurs in Habrobracon if mated females are X-rayed. This may be due to a greater proportion of dominant lethal chromosomal abnormalities induced in the sperm than in the eggs.

WHITING (1936), using parental stocks that were unrelated to each other, has recently reported dominant lethals resulting from treatment of sperm with neutrons. In this case biparental males were lacking, all zygotes being potentially female-producing. The number of females was markedly decreased without any compensating increase in that of impaternate males.

The following experiments involving egg counts were undertaken in order to have a check on viability which would not be possible from counts of adults alone. Females of an orange eyed stock (11-0) were used; some were bred as virgin, others were mated to treated and to control males of an unrelated wild type stock (25). Such a cross obviates the difficulties due to differences in relative viability of females and biparental males. Only females of relatively uniform viability develop from fertilized eggs.

TABLE 1

Egg counts and offspring from orange stock (11-0) females bred as virgin or mated with X-rayed and with control wild-type males, which were either unrelated (stock 25) or closely related (stock 11).

GROUPS	NO. FEMALES	DAYS	TOTAL EGGS	EGGS PER DAY	PROGENY			PERCENTAGE WITH STANDARD ERRORS OF EGGS PRODUCING		
					o ♂♂	+ ♂♂	+ ♀♀	o ♂♂	+ ♂♂	+ ♀♀
Experiment A 23–29°C										
Unmated	6	136	1511	11.1	806			53.33 ±1.28		
× stock 25 (untreated)	3	67	976	14.6	151		328	15.47 ±1.16		33.61 ±1.51
× stock 25 (5000 R.)	1	14	204	14.6	29		19	14.22 ±2.45		9.31 ±6.43
×stock 11 (untreated)	2	29	285	9.8	50	7	25	17.54 ±2.25	2.46 ±0.92	8.77 ±1.68
×stock 11 (3750 R.)	2	66	889	13.5	254	2	30	28.57 ±1.52	0.23 ±1.58	3.37 ±1.91
×stock 11 (5000 R.)	1	14	179	12.8	52	4	5	29.05 ±3.39	2.3 ±1.11	2.79 ±1.23
Experiments B-C 20–24°C										
Unmated	8	87	759	8.7	189			24.90 ±1.57		
×stock 25 (untreated)	7	82	1005	12.3	95		215	9.46 ±0.93		21.39 ±1.29
×stock 25 (7500 R.)	11	122	1008	8.3	54		5	5.36 ±0.71		0.50 ±0.22
×stock 11 (untreated)	10	100	1004	10.0	105	9	110	10.46 ±0.97	0.90 ±0.30	10.96 ±0.99
×stock 11 (5000 R.)	6	78	729	9.3	62	3	23	8.50 ±0.10	0.41 ±0.24	3.16 ±0.65

Crosses were also made between 11-0 females and closely related stock 11 males; in this case differential maturation breaks down and male-producing zygotes, XX and YY, are formed as well as female-producing zygotes, XY. It seemed likely that X-radiation might cause a shift in ratio of homeosyngamic fertilization, X with X or Y with Y, as compared with heterosyngamic X with Y, as shown by ANDERSON (1936) for temperature differences.

Egg counts were made with a modification of the methods devised by A. R. WHITING, C. H. BOSTIAN and R. L. ANDERSON. For X-raying a Coolidge water-cooled tube with tungsten target was used at 165 KV and constant potential giving an accuracy within ten percent of the recorded dosage.

Experiment A was performed from April to May, 1936, experiments B and C from October 1936 to January 1937. Experiments B and C are summarized together in Table 1, since there was no significant difference in conditions or in results. Experiment A had a slightly higher temperature range and it is probably for this reason that the egg productivity per female per day (column 5) is slightly higher (average 12.1 —) than in Experiments B and C (average 9.6). It seems likely that stock 11-0 underwent a deterioration in viability between the times of Experiments A and B, reducing the offspring from unfertilized eggs (percentage producing orange males from unmated mothers, Column 9) from 53.3 to 24.5 percent. This reduction in viability of the impaternate males, occurring in some fraternities but not in all, makes conclusions uncertain concerning the number of eggs fertilized in Experiments B and C. Standard errors based on the total number of items (individuals) are not adequate measures of reliability when such items occur in groups (fraternities). If viability of unfertilized eggs averaged the same in all cases so that the same proportion of impaternate males developed, we could tell what proportion of eggs were fertilized and thus also determine the viability ratio of the females.

From offspring of unmated females in Experiment A, the viability of unfertilized eggs appears not far from fifty percent. Crosses with untreated individuals of the unrelated stock 25 show that about fifteen percent of eggs develop into impaternate males; therefore thirty percent were unfertilized. Of the remaining seventy percent about forty-eight percent develop into females. Female viability is therefore not greatly different from that of males.

Applying the same reasoning to Experiments B–C where viability of unfertilized eggs is only about 25 percent, we find about sixty percent of the eggs were fertilized by untreated stock 25 sperm and show thirty-three percent female viability. These conclusions are unreliable because of the occurrence of low viability factors and the small number of fraternities.

X-radiation of stock 25 sperm gives a marked decrease in female progeny, a decrease of sixty-six percent for 5000 R (Experiment A) and ninety-seven percent for 7500 R (Experiments B–C). There is no compensating increase in males and hence we are dealing with induction of dominant lethals rather than with inactivation of sperm.

In crosses with closely related stock 11 males, three classes of progeny are produced instead of two. The breakdown of differential maturation as a result of close parental relationship permits the formation of relatively inviable XX and YY combinations, a few of which develop into biparental males. The percentage of eggs producing females is significantly

lowered in both sets of experiments when stock 11 males are used, and it is further lowered by X-raying of such males. In Experiment A there appears to be an increase in impaternate males after treatment, but this statement cannot be made definitely since the number of fraternities is very small. If both sets of experiments be averaged, females develop from 10.5 percent of eggs fertilized by untreated males, 3.6 percent from those fertilized by males treated with 3750 R and 3.1 percent from those fertilized by males treated with 5000 R. The number of biparental males is too low to show any significant influence of radiation comparable to that occurring in their sisters. It can only be said that they are neither totally eliminated nor are they greatly increased.

These tests, although based on actual egg counts rather than on offspring per vial, thus far merely corroborate STANCATI'S conclusion that X-raying of sperm induces dominant lethals. Whether such treatment can inactivate the sperm, reducing the percentage of eggs fertilized, or whether it can modify the type of fertilization, changing the ratio of heterosyngamic (X with Y) and homeosyngamic (X with X or Y with Y) fertilization are still open questions.

The author is indebted to Dr. RAYMOND ZIRKLE of the Department of Radiology, University of Pennsylvania Hospital, for giving the X-ray treatments, to Dr. P. W. WHITING for suggesting the problem and to the Committee on Effects of Radiation on Living Organisms (National Research Council) who have made the work possible through grants to Dr. WHITING for technical assistance. The breeding work was carried out at the Zoological Laboratory of the University of Pennsylvania.

SUMMARY

Eggs were counted and the progeny recorded from females which were bred as virgins or were mated to unrelated or to related males. Untreated males or males treated with X-rays were used as parents.

The percentage of eggs producing progeny was not decreased in the lay of outcrossed females as compared with that of virgin females, but percentage of eggs producing daughters was greatly decreased when mothers were mated to related males as compared with those mated to unrelated males.

If crosses were made to treated males which were either related or unrelated, the percentage of eggs producing females was greatly decreased and there was no compensating increase in impaternate males. This is interpreted as an indication of the production of dominant lethals rather than inactivation of sperm and is consistent with the results of STANCATI. There was no significant effect of the treatment on production of biparental males.

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